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Strong tilt illusions always reduce orientation acuity

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ABSTRACT

The apparent spatial orientation of an object can differ from its physical orientation when differently oriented objects surround it. This is the "tilt illusion". Previously [Solomon, J. A., & Morgan, M. J. (2006). Stochastic re-calibration: Contextual effects on perceived tilt. *Proceedings of the Royal Society of London. Series B, Biological Sciences, 273*, 2681–2686], we reported a loss of orientation acuity whenever a large physical tilt was required to compensate for the tilt illusion and make a target appear horizontal. Since all of those targets appeared to be at least approximately horizontal, we concluded that orientation acuity was not wholly determined by the target's apparent orientation. In the present study, we used oblique (i.e. neither horizontal nor vertical) reference orientations to more directly examine the effect of perceived orientation on orientation acuity. The results show that when surround and reference were parallel, there was no tilt illusion and acuity was high. Acuity suffered whenever the tilt illusion caused a large discrepancy between the target's physical and perceived tilts. Since this was true even for tilted references, context-induced acuity loss cannot be simply an "oblique effect" of the target's physical orientation.

1. Introduction

A visual target's immediate context can have a huge impact on the way it looks. The most famous contextual effects are those that produce systematic biases in appearance. Fig. 1 contains an example. When the vertically oriented target appears within a differently oriented surround, the visual system exaggerates the difference (i.e. contrast) between their orientations (Gibson, 1937). Because of this *tilt illusion*, the target must be given a small tilt in the direction of the surround in order to appear vertical.

Another effect of the tilted context in Fig. 1 is acuity loss. When a target is surrounded by obliquely oriented stimuli, decisions regarding whether its orientation is clockwise (CW) or anti-clockwise (ACW) of vertical or horizontal are less consistent than when it is surrounded by vertical, horizontal or no stimuli (Solomon & Morgan, 2006).

Orientation acuity is known to be affected by various factors other than context, notably the spatial orientation of the target. Acuity for obliquely oriented targets is significantly worse than acuity for horizontal or vertical targets (Appelle, 1972). With no evidence to the contrary, it could be supposed that acuity was reduced for obliquely surrounded targets simply because we (Solomon & Morgan, 2006) had to physically tilt them, in order to compensate for the tilt illusion. Below we describe an experiment designed to test this possibility.

Here, it should be noted that we are not the first to examine how acuity depends on the contrast between centre and surround orientations. Meng and Qian (2005) fixed the physical orientations of their targets (at vertical ± 5°) and recorded higher acuities when more oblique surrounds made these targets seem closer to vertical than when near-vertical surrounds made them seem more oblique. From these results we can conclude that acuity cannot be determined solely on the basis of a target's physical orientation; however Meng and Qian never checked whether changes in physical orientation would affect acuity when the perceived orientation remained constant. An adaptive staircase (described below) was exploited in an earlier study (Solomon & Morgan, 2006) to fix the apparent target orientations just-noticeably CW or ACW from horizontal. As previously noted, we recorded lower acuities when these targets required physical tilts to compensate for the effect of oblique surrounds on orientation bias. Thus orientation acuity cannot be determined solely on the basis of a target's apparent orientation either.

2. Main experiment: methods

2.1. Observers

There were three observers: the first author (JAS) and two graduate students. Both students were experienced psychophysical observers, and one (EG) was naïve to the purposes of the experiment. The latter two observers were examined by an optometrist less than 1 year before this experiment was conducted. Both were deemed to have no refractive error. JAS wore corrective lenses.

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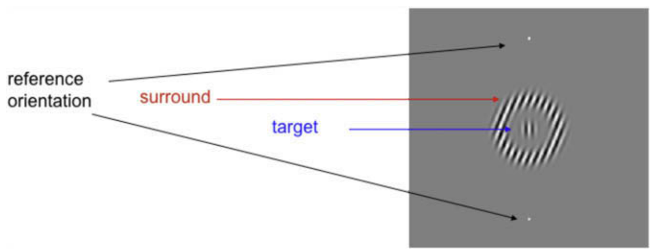

Fig. 1. Example stimulus. Observers had to decide whether the target was CW or ACW of the reference orientation. Trials were blocked according to the reference orientation. Within each block, several different surround angles were interleaved. All stimuli were presented at maximum contrast.

2.2. Apparatus

The Cinematica/Psychophysica software used in this experiment is described elsewhere (Solomon & Watson, 1996; Watson & Solomon, 1997). Observer AT viewed a 55-cd/m^2 display (a Dell M992 CRT) from 95 cm in a well-lit room. JAS and EG viewed a somewhat smaller Dell, emitting an average of 39 cd/m^2 from 82.5 cm. For all three observers, the monitor's resolution was 32 pixels/degree both vertically and horizontally. Observers were free to move their heads and eyes.

2.3. Stimuli

Fig. 1 shows the configuration of all stimuli. The targets were cosine-phase Gabor patterns, whose wavelength and spread were $\lambda = 0.25°$ and $\sigma = 0.18°$, respectively. The target and surround wavelengths were identical. Target and surround were also phase-locked, so that when they had the same orientation, they also had the same spatial phase. (In our previous study, Solomon and Morgan (2006), phase-locked and phase-randomised stimuli produced virtually identical results.) A radial slice through any surround would reveal a Gabor function whose spread was identical to that of the target. The distance between the peak of its Gaussian envelope and that of the target was $3\sqrt{2}\lambda \approx 6\sigma$. This is the same distance used in our previous study. It is twice the maximum distance at which one Gabor pattern can elevate contrast threshold for detecting another in the fovea (Levi, Klein, & Hariharan, 2002). The reference orientation was defined by two white squares [$0.09° \times 0.09°$] on opposite sides of the target. The distance between each and the centre of the target was 3.3°.

2.4. Procedure

On each trial, target and surround were exposed for 100 ms. The reference orientation remained visible throughout each block of 160 trials. The observer was required to decide whether the target was CW or ACW of it, and entered his response with a key press. No feedback was given.

Three different reference orientations were used: 0°, 7.5° and 15° CW of vertical. CW (rather than ACW) orientations were selected arbitrarily. It seems unlikely that ACW references would produce qualitatively different results, but we have not actually tested them. More oblique reference orientations were avoided to ensure a monotonic decrease in acuity with reference angle (cf. Regan & Price, 1986). With respect to (w.r.t.) each reference, there were seven surround tilts $s \in \{-45°, -22.5°, -5°, 0, 5°, 22.5°, 45°\}$, and a no-surround condition. Prior to each trial, QUEST (Watson & Pelli, 1983) was used to find the μ that maximized the likelihood that all the previous data collected with the same combination of reference and surround orientations had been generated by the psychometric function

$$P_{\text{ACW}}(t) = 0.01 + 0.98\Phi[(t - \mu)/\sigma]. \tag{1}$$

In the preceding equation, P_{ACW} is the probability of an ACW response, $\Phi[]$ is the standard normal cumulative distribution function, t is the target tilt and $1/\sigma$ is an estimate of the observer's average acuity for that reference angle, based on responses collected in previous blocks of trials. For JAS and AT, σ was re-estimated after every block. For EG, it was re-estimated after every other block. For all observers, on the first block of trials, σ was set to 2°. Instead of using μ for target tilt, we used $\mu \pm \sigma$. This allows efficient estimates of both bias and acuity. Furthermore, this procedure ensures an equal frequency of CW and ACW responses in each condition.

Due to limited availability, observer EG completed just 18 blocks, for a total of 120 trials with each combination of reference and surround orientation. AT completed 36 blocks. After the first 18, QUEST was re-initialized; σ was set to 2° and t was given a random value. JAS completed 54 blocks. For him, QUEST was re-initialized after both the 18th and the 36th block.

3. Main experiment: results

3.1. Estimates of bias and acuity

For any particular viewing condition, estimates of bias and acuity could be obtained by simultaneously fitting all the data with the psychometric function described in Eq. (1). One potential problem with that approach is that day-to-day fluctuations in bias will masquerade as reduced acuity. This problem can be alleviated somewhat by adopting an alternative approach and geometrically averaging the (independent) estimates of acuity obtained following each initialization of QUEST.

Geometric means, which correspond to the average logarithm, are appropriate because the size of measurement error increases with acuity itself.[1] Use of logarithmic axes in the figures below is appropriate for the same reason. They are required for the confidence intervals to be roughly symmetric about each estimate of acuity.

Unlike that for acuity, the measurement error for bias does not necessarily increase with bias itself. Accordingly, we use linear axes for bias. The symbols in Fig. 2 represent the arithmetic means of independent bias estimates and the error bars (in every case smaller than the symbol size) contain four standard errors of this mean, as computed from the same samples. Unlike acuity, this average bias cannot be very different from a single estimate obtained by simultaneously fitting all the data. Since we have only one independent bias estimate for EG in each condition, bootstrapping (Efron, 1979) was required to estimate each 95% confidence interval. This was accomplished by simulating all 120 trials 40 times and discarding the highest and lowest estimates.

In overall magnitude, EG's biases were mostly smaller than JAS's, which were mostly smaller than AT's. However, in all cases, the relationship between surround orientation and bias was similar to our earlier findings with similar stimuli (Solomon & Morgan, 2006). Specifically, all the biases effectively exaggerated the difference between target and surround, and the largest magnitudes were obtained with ±22.5-deg surrounds.

We turn next to acuities. Fig. 3 shows acuities in the no-surround condition as a function of the reference orientation. Our data confirm the oblique effect, (e.g. Appelle, 1972), i.e. acuity decreased as the reference orientation became more oblique.

[1] A Mathematica notebook (Wolfram, 2003), containing a demonstration of the rough proportionality between acuity and the standard deviation of acuity estimates, can be downloaded from http://www.staff.city.ac.uk/~solomon/slopeScatter.nb.

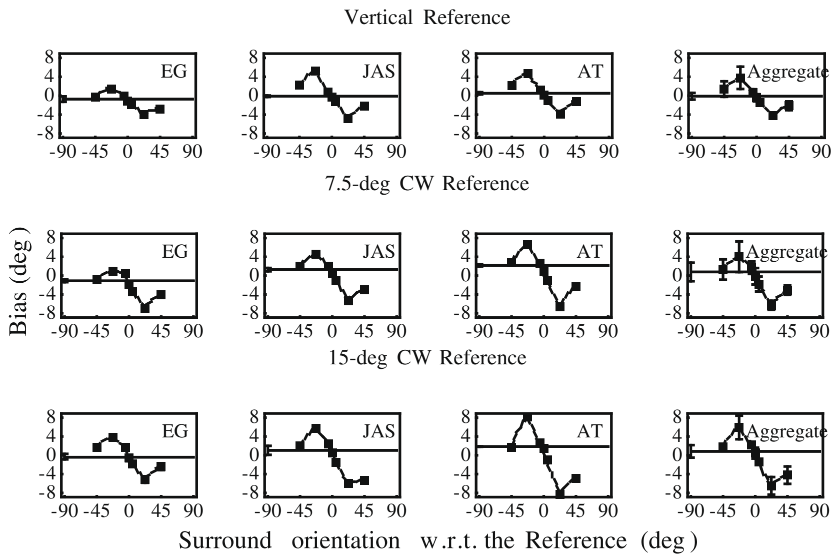

Fig. 2. Observer biases. CW orientations are positive, ACW orientations are negative. Horizontal lines indicate biases in the no-surround conditions. Error bars contain 95% confidence intervals. Most are smaller than symbol size. All biases effectively exaggerated the difference between target and surround, i.e. the target required a tilt toward the surround in order to appear aligned with the reference. Maximum biases were obtained with ±22.5-deg surrounds. The rightmost column contains aggregate data. Each symbol reflects the mean of all three observers. Error bars contain four standard errors of this mean.

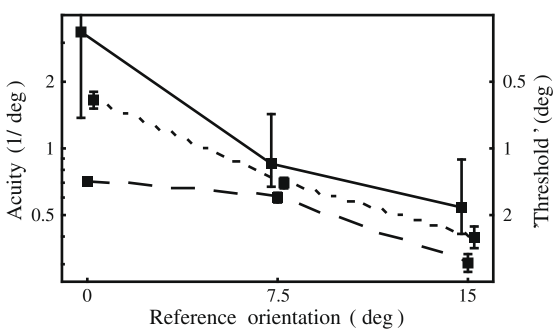

Fig. 3. The oblique effect for orientation acuity. All data come from the no-surround condition. Solid, dashed and dotted curves illustrate acuities for EG, JAS and AT, respectively. 'Threshold' (i.e. the reciprocal of acuity) is indicated on the right-hand axis.

Acuities from all conditions are plotted Fig. 4. (Data from Fig. 3 are re-plotted as horizontal lines.) From the figure it is clear that acuity also decreased with reference tilt when the surround was parallel to the reference, although not quite so dramatically as it did in the no-surround condition. Consequently, with the most oblique reference orientation (15°), acuity was much better with a surround parallel to the reference than it was with no surround. Although the biases with −5° surrounds were significantly different from those with +5° surrounds (confidence intervals do not overlap in Fig. 2), for any given reference orientation there were almost no significant differences between the acuities with these surrounds. The one exception can be found in JAS's data with the 15° reference. The acuities with these slightly tilted (w.r.t. the reference) surrounds were also almost always greater than those with the more tilted (±22.5° and ±45°) surrounds, the only exception being found in EG's data with the vertical reference.

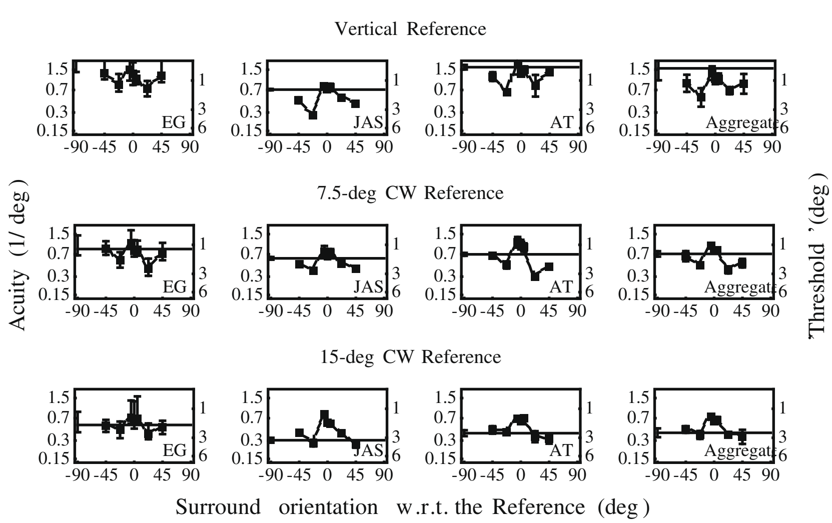

Fig. 4. Observer acuities. Layout analogous to Fig. 2. Acuity decreases with reference tilt. It is particularly poor when the surround is oriented ±22.5° with respect to the reference. NB: EG's poorly constrained no-surround acuity with the vertical reference is not visible, but the lower limit of the 95% confidence interval for this acuity is illustrated by the error bar in the upper left-hand corner.

Table 1
Regression Analyses Best fits in bold-face type.

		Bias fluctuations proportional to bias: $b = \lvert\mu_{r,s}\rvert$					Bias fluctuations proportional to the tilt illusion: $b = \lvert\mu_{r,s} - \mu_{r,0}\rvert$				
		Interactions allowed			No interactions		Interactions allowed			No interactions	
		$p_{\text{interaction}}$	p_{bias}	r^2	p_{bias}	r^2	$p_{\text{interaction}}$	p_{bias}	r^2	p_{bias}	r^2
Perceived tilt: $t = r$	EG	0.955	0.012	0.823	<0.001	0.823	**0.275**	**0.002**	**0.831**	<0.001	0.818
	JAS	0.834	0.017	0.570	<0.001	0.568	0.732	0.015	0.575	<0.001	0.572
	AT	0.038	<0.001	0.807	<0.001	0.750	**0.006**	**<0.001**	**0.856**	<0.001	0.774
Physical tilt: $t = \lvert r + \mu_{r,s}\rvert$	EG	0.375	<0.001	0.794	<0.001	0.784	0.041	<0.001	0.767	<0.001	0.700
	JAS	0.855	0.017	0.559	<0.001	0.558	**0.947**	**0.023**	**0.588**	0.001	0.588
	AT	0.008	<0.001	0.737	<0.001	0.599	0.004	<0.001	0.806	<0.001	0.686

One aspect of these results not seen in our previous work is the idiosyncratic nature of JAS's performance. EG's and AT's acuities were lowest when the surrounds were tilted ±22.5° w.r.t. the reference, and when that reference was 15° CW of vertical, their acuities with ±45° surrounds were almost as bad. JAS's results with ACW surrounds were similar, but his acuity with +45° surrounds was always worse than that with +22.5° surrounds. Moreover, with the vertical reference, JAS's acuity with the −22.5° surround was much worse than his acuity with the +22.5° surround, despite the fact that both of these surrounds produced biases of similar magnitude. At present we are unable to offer any explanation for his asymmetrical performance.

3.2. Regression analyses

Recall that our procedure forced all targets to be just-noticeably tilted (CW or ACW, with equal frequency) w.r.t. the reference. Thus, on average, the target was perceived to be parallel with the reference, regardless of its surround. If acuity were wholly determined by the perceived target orientation, then only the reference orientation should have mattered, and all the symbols in each panel of Fig. 4 should have fallen on a horizontal line. Our data are clearly inconsistent with this prediction. One logical alternative is that the target's physical orientation determines acuity.

Yet another alternative is that the oblique effect is just one contributing factor to orientation acuity when the perceived and physical tilts are different. Acuity may also reflect a fluctuation in bias (Solomon & Morgan, 2006). To examine the influence of both factors on acuity, we have performed several regression analyses.

Each regression effectively assumes that log acuity decreases linearly with the target's average perceived or physical tilt. Our use of the logarithm is once again necessary because the standard deviation of our acuity estimates increases with acuity itself. Without the logarithm, homoscedasticity would be lost, and homoscedasticity is a requirement for the regression analyses described below (Hays, 1988).

Since orientation is cyclic, our assumption cannot be true of all targets, but it is a reasonable first approximation within the restricted range (0–20° w.r.t. vertical) we consider here. As previously noted, the average perceived tilt is simply the reference orientation. The average physical tilt can be computed by subtracting the bias ($-\mu$ in Eq. (1)) from the reference.

We also assume a linear effect of fluctuating bias on acuity, but we have no way of directly measuring that fluctuation. It may depend solely on bias amplitude, in which case we could assume that any effect of bias fluctuation should be proportional $|\mu|$. One problem with this assumption is the fact that biases exist even when there is no tilt illusion (e.g. when the surround and reference are parallel). Consequently, the tilt illusion can actually reduce bias. If bias fluctuation depends on the tilt illusion, we can assume that it is proportional to $|\mu - \mu_{r,0}|$, where $-\mu_{r,0}$ is the bias measured when the surround has zero tilt w.r.t. reference orientation r. Without a strong argument in preference for either of these alternatives, we adopted both, and performed separate analyses. A similar solution ended our struggle to decide whether or not a term for interaction was appropriate. That is, we decided to do separate analyses, both including and excluding the possibility of interaction. Generally, our regression contours minimize the sum of squared errors $\sum_{r,s} e_{r,s}^2$ in the equation

$$-\log \sigma_{r,s} = a_0 + a_1 t + a_2 b + a_3 t b + e_{r,s}, \tag{2}$$

where t, b and $1/\sigma_{r,s}$ are the mean target tilt, the size of the tilt illusion and the acuity measured with reference orientation r and surround tilt s.

As previously discussed, there are two possible interpretations of t. It is either the reference orientation r, which was never negative (i.e. ACW), or the difference between the reference and the bias $|r + \mu_{r,s}|$. Also previously discussed are the two possible interpretations of b. It is either $|\mu_{r,s}|$ or $|\mu_{r,s} - \mu_{r,0}|$. For each observer, all four combinations of these interpretations were tested twice: once allowing all four parameters a_0, a_1, a_2 and a_3 to vary freely, and once excluding the possibility of interaction (i.e. forcing $a_3 = 0$). Statistics appear in Table 1.

To reiterate our null hypothesis, if acuity were wholly determined by the oblique effect, we would not expect the size of the tilt illusion to account for any additional variance in acuity. But it does, significantly. Regardless which combination of assumptions was used, the analyses all suggest clear evidence ($p < 0.025$) for a main effect of bias fluctuations on acuity.

In Table 1, goodness-of-fit is indicated by the value of r^2, which ranged from 0.56 to 0.86. For two of the three observers (EG and AT), acuities were consistently better correlated with the target's perceived tilt than they were with its physical tilt. Best fits were obtained when bias fluctuations were assumed to be proportional to the size of the tilt illusion and interactions were allowed. This analysis is illustrated in Fig. 5.

One final noteworthy statistic is the maximum acuity that can be obtained with a large tilt illusion. The tilt illusion reached 7° in all three observers. From the regression contours drawn in Fig. 5, we can infer that with an illusion this size, the maximum obtainable acuity (i.e. when the target is apparently vertical) is just 25% (EG), 37% (JAS) or 20% (AT) of what it would be without a tilt illusion.

4. Control experiment: methods

Although the main experiment makes clear that oriented surrounds affect orientation acuity, it does not make clear whether it is only the surrounds' orientation content that is responsible for this effect. The control experiment we now describe was necessary to determine whether acuity would even be affected by an isotropic surround. Since this control experiment was performed several

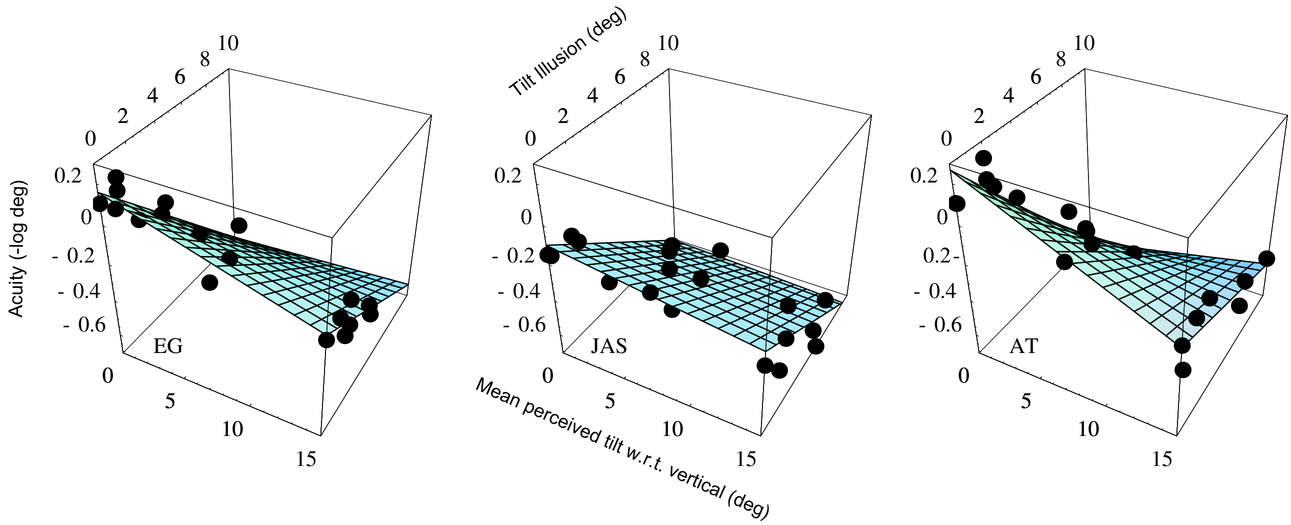

Fig. 5. Simultaneously regressing acuity against the target's apparent tilt and the size of the tilt illusion. Each point represents a unique combination of surround and reference orientations. Due to the nature of our adaptive procedure, the target's mean perceived tilt is simply the reference orientation. The size of the tilt illusion is defined as the unsigned difference between bias with a tilted surround and bias when the surround and reference are parallel. All regression contours all slope down toward high tilts and large tilt illusions.

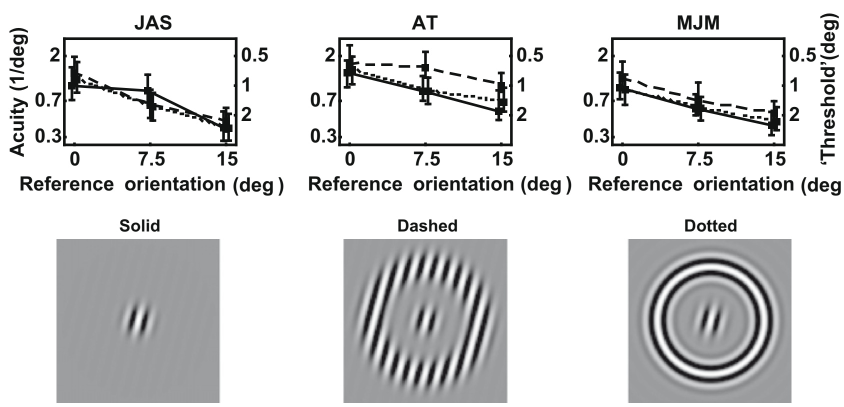

Fig. 6. The effect of parallel and isotropic surrounds on acuity. The lower panels show the three types of surround (none, parallel and isotropic). The parallel surround was always parallel with the reference orientation. Whereas acuities with this latter type of surround (dashed lines) were sometimes enhanced, there was no difference between acuities with isotropic and no surrounds (dotted and solid lines, respectively). Error bars contain 95% confidence intervals.

months after the main experiment, we decided to replicate our previous findings with both parallel surrounds and no surrounds. This was to ensure that acuity had not changed drastically in the intervening months. The methods were identical to those of the main experiment with the following exception: both authors and AT served as observers. The isotropic surround appears in Fig. 6.

5. Control experiment: results

Fig. 6 shows summarizes all the data collected from JAS and MJM (1080 trials each), but AT required significant re-training. Fig. 6 shows the last 1080 of his 3240 trials. For all three observers, performances with the isotropic surround were virtually identical to performances without any surround. We can thus be confident that it is the orientation content in oblique surrounds that is responsible for their effects on orientation acuity.

6. Discussion

Inhibition between cortical neurons having adjacent receptive fields and a similar preference for orientation can readily produce the exaggeration of orientation contrast known as the tilt illusion (see Howard (1982) for a review). Seemingly inconsistent with this simple story is our earlier finding that horizontal surrounds do not reduce acuity for apparently horizontal targets (Solomon & Morgan, 2006). Indeed, our current results suggest that, if anything, orientation acuity increases whenever the target and its surround have similar tilts.

Another way of putting this is that in central vision, surrounds reduce acuity only when forming oblique angles with the target. The visual system exaggerates these angles and thus slightly tilted targets may appear to be nearly vertical when surrounded by a more oblique grating. Nonetheless, we have found that acuity for these apparently vertical targets is less than it would be if these same targets were surrounded by a parallel grating (cf. Meng & Qian, 2005).

Our results allow us to be confident that strong tilt illusions reduce acuity, but we cannot be certain that all tilt illusions reduce acuity. In particular, we did not examine the effects of surrounds forming angles greater than 45° with the reference. Consequently, we as yet do not know whether the an acuity loss is also associated with the small, "indirect" tilt illusion, which is sometimes obtained when surround and target differ by ~75° (Wenderoth & Johnstone, 1988).

The tilt illusion may be caused by neurophysiologic shifts in orientation preference, rather than lateral inhibition (Gilbert & Wiesel, 1990). If this recalibration were to fluctuate from trial to trial, acuity would suffer (Solomon & Morgan, 2006). Large fluctuations would outweigh any benefit from making the target appear more vertical.

The oblique effect is thought to be consistent with physiological studies showing that relatively few neurons are tuned to oblique orientations (Mansfield, 1974). An alternative theory is that stochastic recalibration is responsible for our inferior acuity with oblique stimuli (Morgan, 1991). In two studies, Andrews (1965, 1967) recorded large, constant errors (i.e. biases) when observers were asked to compare a briefly flashed, short line segment with a longer, continuously visible, oblique line. In one study (1965), the errors tended to be in the direction away from the cardinal axes. In the other, the errors went in the opposite direction. This apparent inconsistency may be real. That is, even in the same observer, biases may fluctuate, resulting in a loss of orientation acuity. The experiments described above do not support one theory of the oblique effect more than any other. They were designed strictly to disentangle the acuity loss associated with the tilt illusion from that caused by the oblique effect.

Tilted contexts may thus merely intensify a natural inconsistency in our ability to make orientation judgments. That inconsistency may or may not be least when the target appears to be aligned with a cardinal axis, but it is clear from our results that any time a tilted context to perturbs apparent tilt away from physical tilt, there will be an additional loss of orientation acuity.

Acknowledgments

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